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The Internal Structure of Ovicells in Salmonidae and Coregonidae and the Taxonomic Status of These Groups of Fishes

by

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During the period of trophoplasmic growth, the oocytes of Salmonidae (genus Salvelinus, Salmo, Oncorhynchus) and Coregonidae (Coregonus) are distinguished by the place and time of occurrence of polysaccharide and lipide vacuoles, their dimensions, distribution, relative and absolute number, the structure of their yolk, and a series of other indicators. The characteristics of the internal structure of the ovicells permitted the conclusion to be drawn that the differences between Salmonidae and Coregonidae attain the rank of family.

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At the present time, there are two views regarding the taxonomic status of whitefish. Some authors regard the group as a subfamily, Coregoninae, of the family Salmonidae

*The figures in the right-hand margin indicate page numbers in the original (Tr.).

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(Nikol'skii, 1971; Svetovidov et al., 1975); others consider it an independent family, Coregonidae (Pirozhnikov et al., 1975; Reshetnikov, 1980; Soin, 1980, and others). It should be mentioned that various methods have been used to determine the taxonomic status of this group: embryological, morphological, biochemical, genetic and paleontological (see Reshetnikov's summary, 1980). To this date, however, there is still no unified opinion on the matter.

The present paper is an attempt to determine the rank of the differences between the Salmonidae proper, and the Coregonidae, based on a study of the internal structure of ovicells at various stages of growth.

Materials and Methods

Fixed salmon ovaries at various stages of maturity (Sakhalin or Arctic char, freshwater and anadromous malma, masu, Ob whitefish, Siberian cisco) served as material for the experiment. The malma were taken from the Pervukhina River (Kunashir Island); the char and masu were taken from the Kievka River and Kievka Bay in the Primor'e region; the whitefish were taken from the Anadyr River basin (Chukotka). Pieces of the gonads were fixed in Bouin's solution, Carnoy's fixative, FSU [I was unable to verify this term - Tr.], and 10% neutral Formalin; they were then immersed in parafin, and 5-7 μm sections were prepared. The sections were stained with Heidenhain's azan stain.

In order to determine initial and total proteins in the oocytes, the ovarian sections were stained with solid green solution, pH 2.0-2.2 and 8.0-8.2. Mucopolysaccharides (PAS reaction) were determined using MacManus's method (Merkulov, 1969); phospholipides were determined by tinting the sections with Sudan black B.

Results

A cytomorphological analysis of the Salmonid ovaries (Sakhalin or Arctic char, freshwater and anadromous malma, masu) revealed that during the transition of the oocytes from proto- to trophoplasmic growth, "polysaccharide" vacuoles begin to appear in the peripheral section of the sex cells (Fig., a)[1]. 223

The diameter of these vacuoles ranges between 5 and 9 m. Their number and diameter then increase, and in phase D_2 they occupy the external half of the ovicell (Fig., b). Then in Phase D_3, when they have filled almost the entire oocyte, large vacuoles of a lipide nature appear close to the nucleus. Their diameter (Fig., c) is much greater than that of the remaining vacuoles. For example, in the char and malma, the diameter is 20-26 μm; in species of the genus

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[1] Apart from polysaccharides, which make up their bulk, these vacuoles also contain proteins and lipides (Ivankov, Shkarina, 1981).

Oncorhynchus, these vacuoles are still larger. In individuals from the genus Salvelinus (loaches), these vacuoles are arranged at some distance from the nucleus; in salmon of the genera Oncorhynchus and Salmo, the internal lipide vacuoles lie close to the nucleus (Fig., d; see also Lemanova, 1976, Fig. 3).

The relative diameter of the fatty vacuoles (the ratio between the diameter of the vacuole and the diameter of the oocyte) varies between 2.6 and 9%. In loaches the relative diameter of the fatty vacuoles is smaller than in Pacific and Atlantic salmon. In char and malma the relative diameter is 2.7 and 2.6% respectively. For masu, pink salmon and sockeye salmon the values are 4.5, 5.5 and 9%, and for rainbow trout - 4.5%.[2]

The diameters of the polysaccharide vacuoles are not so varied among the various Salmonidae; among loaches, diameters range between 1.6 and 2.1%, and among Pacific and Atlantic salmon - between 1.8 and 2.5%.

Once vacuolization is complete (phase D_3), small lumps of yolk appear on the cytoplasmic bridges between the "polysaccharide" vacuoles in the Salmonid oocytes. These small lumps gradually increase in diameter; they also begin

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[2]The relative diameters of vacuoles in the ovicells of pink salmon, sockeye salmon and rainbow trout were calculated using photographs contained in the works of Ievleva (1968, 1970, 1970a) and Lemanova (1976).

to appear in the vacuoles. These unite into separate small drops, gradually fill the entire oocyte, and finally unite into a single drop.[3]

In Coregonid oocytes, in contrast with those of Salmonidae, the first vacuoles appear either around the nucleus, and then shortly after in the peripheral areas (Siberian cisco), or in both zones at the same time: around the nucleus and in the peripheral areas (Ob whitefish) (Fig.). They then increase in number and form two distinct zones: circumnuclear and peripheral (Fig., f). During phase D_2 (the oocyte is half filled with vacuoles), 7-14 rows of vacuoles appear in the first zone, and 1-3 rows in the second zone (Table). The interior vacuoles are of a lipide nature (Fig., g) and the exterior vacuoles are mucopolysaccharide. The number of vacuoles then increases (for the most part through an increase in the number of lipid vacuoles), and in phase D_3 almost all of the oocyte is filled with vacuoles. Only a narrow band of cytoplasm situated between these two zones of vacuoles remains free.

It is worth noting that the vacuoles in the circumnuclear zone are of a lipide nature in other whitefish as well (Lapitskii, 1949). In fact they are similar to the lipide vacuoles in Salmonidae. In contrast with Salmonidae,in

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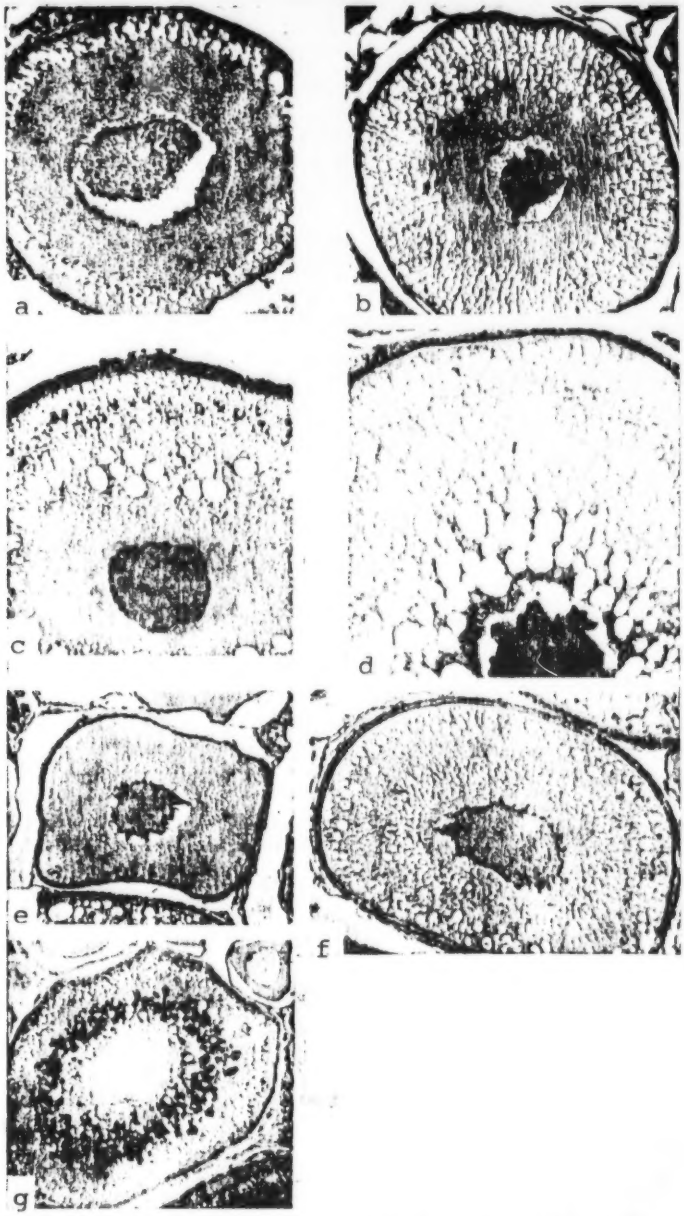
3 For more detail see Ivankov and Shkarina (1981)

which the circumnuclear lipide vacuoles are significantly larger than the peripheral ("polysaccharide") vacuoles, in Coregonidae the circumnuclear vacuoles are smaller (Table). Their average diameter in whitefish and cisco is 8.4 and 9.3 μm respectively, while in malma and char, their diameters vary between 20.5 and 25.6μm.

Here it should also be mentioned that the lipide vacuoles in Coregonidae are significantly smaller than the mucopolysaccharide vacuoles. The relative diameter of lipide vacuoles in the whitefish oocytes in phase D_3 was 1.9%, 224
while that of mucopolysaccharide vacuoles was 2.5%; for cisco the values were 1.7 and 4.6% respectively. It will be recalled that in Salmonidae quite the reverse is true - the fatty vacuoles are much larger (Table).

From the Table it can be seen that by phases D_2 and D_3, the whitefish oocytes were filled for the most part with vacuoles belonging to the internal zone (lipide); the mucopolysaccharide vacuoles were arranged in 1-3 rows on the periphery of the cell. Among Salmonidae, in contrast, the lipide vacuoles appear only when most of the cytoplasm in the ovicell is filled with "polysaccharide" vacuoles.



Oocytes of Salmonidae (a-d) and Coregonidae (e-g) at various stages of trophoplasmic growth: a - freshwater malma in stage D1 (polysaccharide vacuoles begin to appear on periphery); b - Sakhalin or Arctic char in phase D2 (polysaccharide vacuoles occupy external half of cell); c - Sakhalin or Arctic char in phase D3 (large lipide vacuoles visible in zone near nucleus); d - masu in phase D3 (lipide vacuoles immediately adjacent to nucleus); e - Ob whitefish in phase D1 (two zones of vacuoles visible: circumnuclear and peripheral); f - Siberian cisco in phase D2 (two distinct zones of vacuoles visible); g - Ob whitefish in phase D3 (reaction of vacuoles in circumnuclear zone to lipides clearly visible). Magnification: a, e, f - lens 40X, eyepiece 7X; b, g - 20X, 7X; c, d - 10X, 7X

Indicators	Ob whitefish	Siberian cisco	Char	Malma
Site of first vacuoles	Around nucleus and on periphery	Around nucleus	Periphery	Periphery
Number of vacuole bands in phase D2:				
external	2—3	1—2	8—11	7—10
internal	6—9	12—14	none	none
(lipide)				
Vacuole diameters in phase D2, m:				
external	15,5 (11—17)	12,1 (8—14)	15,5 (11—22)	9,9 (6—15)
internal	11 (8—14)	3 (1—6)	none	none
(lipide)				
Vacuole diameters in phase D3, m:				
external	17,6 (14—22)	24 (22—28)	15 (13—19)	16,5 (13—19)
internal	12,3 (8—14)	9,3 (5—14)	25 (22—28)	21 (19—23)
(lipide)				
Diameters of lipide vacuoles in phase E1, m	11 (8—18)	8 (6—11)	33 (18—51)	30 (26—33)
Number of vacuoles on external circumference of oocyte (in phases D2-E1)	80—84	92—120	108—226	118—194

Discussion

Thus the cytomorphological analysis of Salmonid and Coregonid ovicells made it possible to determine that these fish groups differ distinctly in terms of a number of indicators. During trophoplasmic growth, the oocytes of these groups differ in terms of the time and place of occurrence, dimensions, distribution, and relative and absolute number of lipide and mucopolysaccharide vacuoles, the structure of the yolk, as well as several other indicators (see Table and Fig.).

The internal structural peculiarities of sex cells mentioned above are characteristic not only of those species studied by the authors, but also of other species in both the Salmonid and Coregonid groups. Just as in the Siberian cisco and the Ob whitefish, the lipide vacuoles in the oocytes of other Coregonidae also initially appear in the circumnuclear zone. This has been observed in ludoga whitefish, Coregonus lavaretus ludoga, (Lapitskii, 1949), omul, C. autumnalis, (Anisimova, 1952), as well as in chud whitefish, C. lavaretus maraenoides, and ripus, C. albula ladogensis, that have become acclimitized in the Urals (Kharchenko, 1972).

On the other hand, the type of structure observed by the authors in such Salmonidae as Sakhalin or Arctic char, freshwater and anadromous malma, and masu, is also

characteristic of other representatives of that family. In order to be convinced of this, it is sufficient to analyze the data presented in works dealing with the oogenesis of 226
pink and Siberian salmon (Jamamoto et al., 1959; Ishida et al., 1961; Sakun, 1965; Ievleva, 1968), as well as salmon of the genus Salmo (Lemanova, 1974, 1976).

From an analysis of all the available materials and secondary data, it may be concluded that there is a distinct division between the two groups of Salmoniformes examined above: the first group includes salmon from the genera Salmo, Oncorhynchus and Salvelinus, the second group is made up of Coregonidae (genus Coregonus).

As for the rank of the differences between Salmonidae and Coregonidae, the following should be mentioned: we must agree with Reshetnikov (1980: 145), who said that "...even with a comprehensive analysis of indicators, dividing Salmonidae into families involves a certain amount of subjectivity, and depends on which group of fish is used as the standard (what is considered a "good family")". Thus in order to make an objective judgement about the rank of the differences between the two groups of Salmoniformes, it must be shown that the differences in ovicell structure between Salmonidae and Coregonidae are no less significant than those of fish belonging to families whose rank is no longer in doubt. By way of example the authors analyzed the available data on the structure of ovicells of Gadidae and

Merlucciidae of the order Gadiformes, as well as Siluridae and Bagridae of the order Siluriformes.

A study of the internal morphology of Gadid and Merlucciid ovicells revealed that in the first group, cytoplasm vacuolization is very weak, and the yolk appears in the cell immediately after the formation of the first vacuoles in the peripheral zone. In Merlucciidae, vacuolization is much more vigorous (significantly more pronounced), and the yolk appears after the two distinct zones of vacuoles, peripheral and circumnuclear, have finished forming (Ivankov, Svirskii, 1975). These two zones form almost simultaneously. In the present case, there is a certain similarity between, on the one hand, the differences between the ovicells of fish from the two families belonging to the order Gadiformes (Gadidae and Merlucciidae), and on the other, the differences between Salmonidae and Coregonidae of the order Salmoniformes.

As for Siluridae and Bagridae, the differences in ovicell structure separating these two families of fish are even smaller than those separating Salmonidae and Coregonidae. Among fish from the family Siluridae, on the average around seven rows of polysaccharide vacuoles appear in the oocyte before the yolk develops, while in Bagridae, one or two rows appear. It will be recalled that there is also a considerably greater number of rows of polysaccharide vacuoles (7-11) in Salmonid oocytes shortly before the yolk appears, than in those of Coregonidae (1-3 rows).

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THE INTERNAL STRUCTURE OF EGGS IN THE SALMONIDAE AND CORE GONIDAE AND TAXONOMIC STATUS OF THESE GROUPS OF FISHES

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Summary

During the period of trophoplasmatic growth the oocytes of the salmonid (*Salvelinus, Salmo, Oncorhynchus*) and coregonid (*Coregonus*) fishes differ from each other in the place and time of appearance of polysaccharide and lipid vacuoles, their size, position, relative and absolute numbers, yolk structure, and some other features. A conclusion was drawn that the differences in the internal egg structure between these groups attain the familial rang.